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Alteration of Central Metabolism During Plant Adaptation to Abiotic Stresses (Review)

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Plant tolerance to environmental stresses is a polygenic trait, and adaptation to stressful environment is regulated at different levels of plant organization. Widely used gene expression profiling not always allows understanding the essence of the adaptive changes, because of multilevel regulatory processes involved in adaptation. Therefore, an analysis of alterations in metabolites in plants undergoing the adaptation to the stressful environment, probably, is the most adequate approach capable of revealing a complex picture of adaptive responses. Here the information about metabolic adjustments during plants adaptation to abiotic stresses is given with emphasis on waterlogging stress.

Keywords: C*entral metabolism, metabolite profiling, abiotic stresses, stress tolerance*

A large part of soils all over the world is subjected to flooding or waterlogging, which has a strong negative impact on the soils quality and crops. During temporary waterlogging, which is a very common scenario in agricultural practice, water saturates soil for a period of time, wherein roots and lower plant parts are subjected to excessive water while upper parts of plants remain above the water. All plant organs, including aerial, experience severe stress during waterlogging and after waterlogging is withdrawn. Waterlogging alters organic and inorganic composition of soil and accessibility of nutrient, changes the microbial environment, leads to the formation of toxic compounds, and, the most important, it leads to the limitation in available for roots oxygen. Sufficient root oxygen supply is a vital condition for the normal functioning of the plant. The decrease in the level of available oxygen results in alteration of whole-organism metabolism, hormonal status, re-programming of gene expression enabling plants to survive in stressful environment (Blokhina and Fagersted, 2010). Exposure to oxygen following submergence or waterlogging, induces a severe oxidative stress, Reactive Oxygen Species (ROS) formation, resulting in damages to cell structures. Roots responses to waterlogging are more studied and better understood, while the data describing processes occurring in leaves of waterlogged plants are very contradictory. Even in respect to oxygen availability leaf tissue is described by different authors as hypoxic, normoxic, or experiencing oxidative stress. In spite of the significant growing interest to this topic stipulated by its practical importance, not much known about the molecular mechanisms underlying waterlogging and flooding tolerance (van Dongen and Licausi, 2015; Loreti et al., 2017).

Oxygen limitation induces a certain metabolite profile alterations in plant tissue (Borisjuk and Rolletschek, 2009). Accumulation of proteins related to translation and antioxidant defense and an accumulation of a set of enzymes involved in serine, glycine, and alanine biosynthesis from glyceraldehyde-3-phosphate or pyruvate was observed in rice coleoptiles, and accumulation of these amino acids in anoxic rice (Shingaki-Wells et al., 2011). Formation of acetaldehyde and ethanol, accumulation of organic acids, pH lowering are main responses to hypoxia/anoxia. Induction of anaerobic metabolism allows plants to continue ATP supply during a short period of anaerobic conditions (for few hours to few days). Plant leaves are rich in the enzymes necessary for fermentation (Kimmerer and Macdonald, 1987), although till now no correlation between the ability to form acetaldehyde and ethanol and tolerance to flooding was proved, and the order of tolerance did not correlate with root and shoot oxygen content or initial amounts of shoot starch and total soluble sugars (Vashisht et al., 2011). There are contradictory data about oxygen deficiency in leaves of waterlogged plants. In some cases, leaves from root-waterlogged Arabidopsis showed no accumulation of alcohol dehydrogenase and pyruvate decarboxylase mRNA, allowing to assume that leaves did not experience oxygen deficiency (Juntawong et al., 2014). Even when fully submerged under normal illumination shoots tissues remained normoxic (Vashisht et al., 2011; van Veen et al., 2013). Some tolerant species delay or avoid accumulation of ethanol by diverting glycolytic intermediates to alternate end products such as lactate, malate, succinate, y-aminobutyrate,

and alanine (Hook and Crawford, 1978). Typical for anoxic conditions alterations in primary metabolites are characterized by an accumulation of amino acids such as alanine, GABA, and the phosphoesters, glucose-6-phosphate and glycerol-3-phosphate, and other minor sugars (van Dongen et al., 2009; Rocha et al., 2010). Usually, general downregulation of energy-consuming processes under oxygen-limited conditions occurs, when hypoxic signaling pathway is turned on.

Sucrose and glycolysis intermediates. Plant responses to various stresses overlap significantly, and many features of metabolic adaptation are observed in plants subjected to drought, temperature stress, waterlogging or other unfavorable environmental conditions. An increase in sucrose level is one of the most noticeable changes in metabolite profile of plants during adaptation to various stresses, including waterlogging. Levels of raffinose group olygosacharides are also increased in stress-treated plants, as it was shown in many studies. Raffinose, stachyose, and verbascose are osmoprotectants, stabilizers of cellular membranes, scavengers of hydroxy radicals protecting plants from oxidative stress (Nishizawa et al., 2008), are known to accumulate in response to drought, chilling, heat, and high-light irradiation, i.e. all stresses that give rise to excess concentrations of reactive oxygen species (Urano et al., 2009). Raffinose accumulation is regulated by the ABA-independent CBF/DREB1 cold-responsive pathway (Cook et al., 2004) and exhibited an enhanced correlation with dehydration-increased amino acids. Accumulation of raffinose group oligosaccharides in agricultural plants has to be controlled due to their antinutritional properties. The level of myo-inositol, the substrate for mentioned oligosaccharides biosynthesis is also increased in stressed plants. Besides being a substrate for biosynthesis of oligosaccharides and constituents of cell wall (Roberts and Loewus, 1966) inositol is an important metabolic and signaling compound simultaneously, since it plays a role in a phosphate storage, participates in cell-to-cell communication, regulates availability of active auxin in plant tissue and transport (Chen and Xiong, 2010), and coordinates plant responses to salt and dehydration stress (Nelson et al., 1998).

Sucrose synthase route was previously shown in connection with anaerobiosis response (Sturm and Tang, 1999). It was demonstrated that flux via SUS is more important in roots of waterlogged Arabidopsis plants in comparison to ATP-consuming Invertase/hexokinase, but not in seedlings grown on carbon source. Sucrose cleavage through the SUS pathway depends on balanced ratios of UDP/UTP, regulated by nucleoside diphosphate kinase (NDPK) (Bailey-Serres and Voesenek 2008). NDPK activity is enhanced in plant organs under low oxygen (Perata et al., 1996; Guglielminetti et al., 1995), its mRNA is highly expressed in tissues with a low-oxygen microenvironment and high energy demands, such as meristems (Dorion et al., 2006) and seed endosperm (Sanclemente et al., 2016). An increase in UDP-glucose level may be an indicator of hypoxia stress, while under normoxic conditions invertase/hexokinase pathway is a dominant rout.

Tricarboxylic acid (TCA) cycle. A major alteration in TCA cycle intermediates is an accumulation of Succinate. Succinate accumulation is a well-known general plant response to environmental stresses. The addition of succinate salt to the root medium prior to Cu treatment increased the capacity of the maize plants to partially overcome Cu toxicity (Doncheva et al., 2006). A decrease in 2-oxoglutarate level under stress conditions may be an indicator of N deficiency in plants, since the level of 2-oxoglutarate, a key regulator of carbon and nitrogen interactions, decreased under N starvation (Obata and Fernie, 2012). A decrease in the levels of isocitrate was previously observed in plants subjected to high light stress and low temperature. Isocitrate and citrate - an important metabolic branch point, which provides carbon skeletons for nitrogen assimilation and reducing equivalents for biosynthetic reactions, support the functioning of the glyoxylate cycle and the process of gluconeogenesis, and play an important role in the TCA and in energy metabolism, associated with production of secondary metabolites, fatty acid oxidation and biosynthesis (Popova and de Carvalho, 1998). Many enzymes of the tricarboxylic acid cycle such as aconitate, pyruvate-, and 2-oxoglutarate-dehydrogenase are known to be sensitive to oxidative inhibition (Verniquet et al., 1991; Sweetlove et al., 2002), so decrease in mentioned TCA metabolites may indicate that oxidative stress takes place in plants.

Amino acids. Amino acids are not only protein constituents, but also a bridge between primary and secondary metabolism, carriers of nitrogen between roots and above-ground part of plants, precursors of many secondary metabolites, which play role in formation of structural components, and defense (Pratelli and Pilot, 2014). Amino acids profile is altered significantly in stressed plants.

Increase in Ser level is also known to be a general stress response (Rai, 2002). Alanine,

lactate, and GABA were shown as major metabolites increased in 2 hours in response to oxygen deprivation (Mustroph et al., 2014). Increase in Ala and GABA or enzymes involved into these metabolites biosynthesis were described in many cases for oxygen-deprived plant tissue, even under mild hypoxia (Miyashita et al., 2007; Limami et al., 2008). Reverse conversion of alanine to pyruvate during recovery from low-oxygen stress plays a role in Ala reuse after re-aeration (Miyashita et al., 2007). The level of Ala correlates with the intensity of starch catabolism and decreases under oxidative stress conditions. Ala and lactate prevent the accumulation of Pyr in order to avoid inhibition of glycolysis and fermentation (Rocha 2010b). Branched-chain and aromatic amino acids are substrates for many secondary metabolites biosynthesis. Branched-chain amino acids regulate with back regulation hormones gibberellins and IAA (indole acetic acid) (Gao et al., 2009; Parsons et al., 2015). These amino acids (especially leucine) are able to participate in regulation of gene expression (Kimball and Jefferson, 2006; Binder, 2010; Obata and Fernie, 2012), increase in these amino acids level was detected in plants subjected to water deficiency stress, including tomatoes (Semel et al., 2006), grain cultures (Bowne et al., 2012; Witt et al., 2012). Valine is also used for synthesis of proteins and secondary metabolites, accumulation of Val was shown in connection to elevated CO2 concentration in drought-stressed plants, drought stress tolerance (Merewitz et al., 2012), heat shock (Kaplan et al., 2004), and heat tolerance (Jingjin et al., 2012). Shikimate pathway, derived from PEP, a precursor of Pyr, leads to the formation of aromatic secondary metabolites, such as lignin, flavonoids, alkaloids, phytoalexins. These metabolites also have antioxidant property. Aromatic amino acids derived from the shikimate pathway are used in biosynthetic pathways for production of pigments, hormones, and cell wall components. Lignin provides protection against oxygen loss (Bailey-Serres et al., 2012). Shikimate pathway is a major consumer of photosynthetically fixed carbon in vascular plants (Jorgensen et al., 2005; Vogt, 2010). Accumulation of aromatic amino acids in response to biotic and abiotic stresses was previously shown (Kim et al., 2007). Because their biosynthetic pathways have been lost in animal lineages, these amino acids are essential components of the human diet (Maeda and Dudareva, 2012). Both, aromatic and branched chain amino acids are substrates for glucosinolates biosynthesis, defensive compounds, involved in protection against biotic and abiotic stressors in cruciferous (Glawischnig et al., 2003).

Oxaloacetate family amino acids levels, including Asp and Asp-derived Asn and methionine, are decreased under conditions of oxidative stress. Thr and Gly levels remain unchanged under low oxygen conditions (Mustroph et al., 2014). A possible connection between Asparagine-family pathway and Lys-branch was discussed previously, and increase of Asp-family pathway flow into the Lys branch on the expense of flux towards the other branches which leads to the synthesis and further catabolism of Met and Ile was shown (Galili, 2011). Stresses usually suppress the expression of genes encoding biosynthesis enzymes of the Asp-family pathway and stimulate the expression of catabolic genes of the Asp-family pathway.

The observed decrease in the level of Deoxyadenosine, S-adenosyl methionine, S-adenosyl-L-homocysteine can be a result of the deficiency in S and N or intensified consumption of this amino acid. Methionine is a precursor of ethylene through S-adenosylmethionine (Ravanel et al., 1998). Flooding and waterlogging stresses are accompanied by the production of ethylene, which regulates many reactions in response to these stresses (Sasidharan and Voesenek, 2015). Probably, decrease in methionine and related to methionine amino acids levels is a result of these amino acids consumption for ethylene biosynthesis. Methionine also can be used for polyamines biosynthesis. In cruciferous Met and Ala can be also substrates for the major class of glucosinolates biosynthesis.

Most noticeable alteration in a profile of 2-oxoglutarate-derived amino acids is an increase in the level of proline, a well-known stress response metabolite, accumulation of which was documented in response to a range of abiotic stresses. Ornitine and citrulline are possible shuttles of nitrate and carbon between mitochondrion and plastids. Levels of these amino acids are increased in response to low temperature (Cook et al., 2004). Ornitine – can be a source of proline synthesis, since proline in non-stress plants can be toxic for plant cells, ornithine accumulates as a precursor, it is a "gatekeeper" in controlling polyamines and GABA biosynthesis (Majumdar et al., 2016). Citrulline is a nonessential amino acid that is reported to be an efficient hydroxyl radical scavenger and is a strong antioxidant (Akashi et al., 2001; Rimando and Perkins-Veazie, 2005), this amino acid is critical to the detoxification and elimination of unwanted ammonia within cells (Nelson and Cox, 2000). Citrulline accumulation correlates with tolerance to salt and drought stress (Yokota et al., 2002; Kusvuran et al., 2013). Oxidative stress results in a strong decrease in Proline and serine Gln levels, similarly Asp and Asp-derived Asn, homoserine

and Met linked to oxaloacetate and Ala linked to pyruvate is decreased. Adaptation to low-temperature stress is accompanied by increases in ascorbate, ornithine, and citrulline. The accumulation of shikimate, phenylalanine, and fructose, and the decrease of succinate are found in both low temperature and light stress-treated plants (Kaplan et al., 2004; Obata and Fernie, 2012).

His is a chelator of toxic ions (Kramer et al., 1996; Zemanová et al., 2014), important for plant reproduction and growth (Stepansky and Leustek, 2006). His biosynthesis is connected with the pentose phosphate pathway, de novo biosynthesis and salvaging of purines, pyrimidines and the pyridine nucleotide cofactors NAD and NADP (Alifano et al., 1996; Ingle, 2011). Not much is known about the regulation of His level in plant. His biosynthesis process is very susceptible to feedback inhibition. In fungi, regulation of His biosynthesis is tightly coordinated with that of purine biosynthesis and is regulated by adenine limitation (Springer et al., 1996).

Antioxidants. Virtually all biotic and abiotic stresses are accompanied by oxidative stress, including hypoxic/anoxic stress (Pucciariello et al., 2012), and the ability to detoxify activated oxygen species is related to a higher tolerance to environmental stresses. Ascorbate (Asa) and reduced glutathione (GSH) are the main antioxidant components present in most plant cell organelles like mitochondria, chloroplasts, and peroxisomes. Asa can react with reactive oxygen species, such as 1O2, HO· and can act as the substrate for the enzyme ascorbate peroxidase. GSH acts as a cell redox regulator and may act as a ROS scavenger. The balance between GSH and oxidized glutathione (GSSG) is critical for keeping a favorable redox status for the detoxification of H2O2 (Foyer and Noctor, 2011). NAD and NADP play a central role in maintaining plant energy status and redox homeostasis (Hashida et al., 2009). NAD is used primarily in respiratory ATP production whereas NADP is used in reductive biosynthesis. Furthermore, a decrease in the NAD/NADP ratio is tied directly to photosynthetic activity, at least in cyanobacteria (Tamoi et al., 2005). It is also assumed that NADP biosynthesis plays an important role in ROS scavenging.

An adverse effect of stress on plants is also associated with nutrient deficiency (Steffens et al., 2005). Available in the literature data describe an increase in P uptake under waterlogging conditions (Rubio et al., 1997). Severe phosphor (P) deficiency leads to increased levels of phosphorylated intermediates (glucose-6-P, fructose-6-P, inositol-1-P, and glycerol-3-P) and organic acids (2-oxoglutarate, succinate, fumarate and malate). P-deficient plants modify carbohydrate metabolism initially to reduce P consumption and salvage P from small P-containing metabolites, which consequently reduce the levels of organic acid in the TCA cycle (Huang et al., 2008). An increase in the levels of Succinate and malate is a typical feature for P-deficiency stress, also found in waterlogged samples. The observed decrease in purine and pyrimidine derivatives can be a result of N deficiency either. N-uptake could be an important factor in waterlogging tolerance (Kreuzwieser et al., 2002). In general, the combination of the nutrient deficiency and oxidative stress shape the metabolic profile of plant leaves under waterlogging conditions.

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Bitkilərin Abiotik Streslərə Adaptasiyasında Mərkəzi Metabolizmin Dəyişiklikləri (İcmal)

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Bitkilərin ətraf mühitin stress amillərinə davamlılığı poligen xarakter daşıyır. Ətraf mühitin əlverişsiz şəraitinə adaptasiya isə bitki orqanizmlərinin müxtəlif səviyyələrində tənzimlənir. Tənzimləyici sistemlərin çoxpilləli olması hesabına ekspressiya olunan genlərin profilinin geniş tətbiq olunan analizi baş veən adaptiv dəyişiklikləri başa düşməyə imkan vemir. Bu baxımdan, stresə adaptasiya prosesində bitki metabilitlərinin miqdarının dəyişməsinin analizi daha düzgün yoll olub, mürəkkəb adaptiv cavab reaksiyalarını aşkar etməyə imkan verir. Təqdim olunan işdə torpaqda su basmalarınını əsas götürməklə, bitkilərin abiotik stresslərə adaptasiyası zamanı baş verən metabolitik yerdəyişmələr haqda olan məlumatlar analiz edilir.

Açar sözlər: *Mərkəzi metabolizm, metabilitik profilləşmə, abiotik streslər, stresə tolerantlıq*

Изменения Центрального Метаболизма в Процессе Адаптации Растений к Условиям абиотического стресса (Обзор)

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Устойчивость растений к стрессам окружающей среды носит полигенный характер, а адаптация к неблагоприятным условиям окружающий среды регулируется на разных уровнях организации растительного организма. Широко применяемый анализ профиля экспрессируемых генов не всегда позволяет понять суть происходящих адаптивных изменений по причине многоуровневости регуляторной системы, отвечающей за адаптацию. В связи с этим, анализ изменений уровня метаболитов растений, происходящих в процессе адаптации к стрессовым условиям, представляется наиболее адекватным подходом, способным раскрыть сложную картину адаптивных ответов. В данной работе мы проводим анализ данных о метаболических перестройках, происходящих в процессе адаптации растений к условиям абиотических стрессов, с акцентом на стрессе, связанном с затоплением почвы.

Ключевые слова: *Центральный метаболизм, метаболитное профилирование, абиотический стресс, стрессоустойчивость*